REPRODUCTIVE ENERGETICS AND LARVAL STRATEGIES OF NUDIBRANCH MOLLUSCS: EFFECTS OF RATION LEVEL DURING THE SPAWNING PERIOD IN *ONCHIDORIS MURICATA* (MÜLLER) AND *ADALARIA PROXIMA* (ALDER AND HANCOCK)

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ABSTRACT

The nudibranchs *Onchidoris muricata* (Müller) and *Adalaria proxima* (Alder and Hancock) prey preferentially upon the same species of bryozoan, have annual life cycles, semelparous life history strategies and reproduce at much the same time of year. They differ, however, in body size and larval type; the larger *(A. proxima)* reproduces by short-term pelagic lecithotrophic larvae while the smaller *(O. muricata)* has long-term planktotrophic larvae. *O. muricata* allocates absolutely less, but relatively more, energy to reproduction and shows a tight allometric relationship between body size and fecundity. For *A. proxima,* variation in body size explains only ≃ 25% of the variance in individual fecundity, with larger adults producing fewer offspring on a weight for weight basis. Maximization of fitness in *O. muricata* depends, to a large extent, on continued feeding and diversion of assimilated products to current reproduction. *A. proxima* adults appear less able to exploit such recurrent energy, and the suggestion is that this underlies selection for lecithotrophy. (The higher individual larval probabilities of successful metamorphosis conferred by short-term pelagic lecithotropic veligers are presumed to damp the variance in individual fecundity.) This was further evaluated by subjecting both species to differing ration levels (= energy availability) during the reproductive period. The two species responded similarly (on a proportional basis) to ration level, in respect to a range of independently appraised reproductive criteria, but a major contrast was noted for a composite measure of individual daily reproductive 'performance'. *A. proxima* was largely unaffected by ration level, whereas *O. muricata* displayed marked and significant decreases in fecundity, especially on starvation. The implications of the individuals' energetics in explaining selection for particular larval strategies in nudibranch species are discussed.

Three features have become axiomatic within the ecological study of reproductive strategies. First, individual adults will produce as many offspring as possible. Second, individual energy budgets are finite and there are, in consequence, limits to what is possible. Third, there are "costs" associated with expenditure within each component of the budget and, for this reason, we might expect offspring production to be 'optimised', rather than maximised. Within the general framework of life history theory the concept of reproductive "effort" (that is, the proportion of total budget resources diverted to reproductive function) has become a central construct (e.g. Fisher, 1930; Williams, 1966; Tinkle, 1969; Gadgil and Bossert, 1970; Pianka, 1970, 1976; Schaffer, 1974; Stearns, 1976). The energetic costs incurred in reproduction might be most simply envisaged as a reduction in future reproductive potential arising from the diversion of resources away from maintenance, at the expense of possible continued adult survivorship. This principle necessarily extends to consideration of the circumstances which affect and dictate the two fundamental demographic features of the individuals' overall life history strategy; that is, the duration of the adult phase (subannual, annual, biennial or perennial life-cycle strategies) and the frequency of reproductive events [i.e. semelparous (single) or iteroparous (repeated) strategies]. Benthic marine molluscs are perhaps of especial interest to these broader issues, by virtue of their not only displaying the entire spectrum of life-cycle and life history strategies, but also in possessing a variety of pelagic (free-swimming)

or non-pelagic larval forms.

Planktotrophic larvae hatch from small eggs, are 'poorly-developed' and require extended periods feeding and growing in the plankton prior to settlement and benthic metamorphosis (Thorson, 1946). Lecithotrophic larvae hatch from intermediate/large eggs and can be briefly pelagic (but usually non-feeding) or wholly non-pelagic. Thorson (1946) estimated that 80% of benthic marine invertebrates reproduce by means of planktotrophic larvae. This particular feature is, therefore, of some considerable interest, particularly because there are reasons to suppose that planktotrophy is the 'primitive' or 'ancestral' state in a wide variety of phyla (including Mollusca), and, moreover, that the lecithotrophic category is a largely irreversible evolutionary derivative (Strathmann, 1978). What remain to be resolved, therefore, are the selective factors that have dictated such putative evolutionary shifts to the more advanced larval types.

Our investigations have concentrated upon nudibranch molluscs (e.g. Todd, 1979a, b; Todd and Doyle, 1981; Todd and Havenhand, 1983; Hall and Todd, 1986; Havenhand et al., 1986). The rationale of our approach is that energetic considerations outline the bounds of possibility, and that some form of optimisation of individuals' reproductive allocation underlies selection for particular larval types. It is, perhaps, important to emphasize that selection does not necessarily demand efficiency (in terms of numbers of offspring per joule of reproductive allocation): selection ought to favour that strategy which confers the largest number of surviving offspring, even if (perhaps by a particular larval strategy) these are apparently produced "inefficiently" (Todd, 1985). Moreover, functional energetics are not the only parameter in the equation: the differing larval types presumably confer markedly different genetic consequences, especially in terms of individual larval survivorship to metamorphosis, and dispersal potential.

The present paper comprises an extension of previous analyses of reproductive allocation in two species of dorid nudibranchs, Adalaria proxima (Alder and Hancock) and Onchidoris muricata (Müller) (Todd, 1979a; Todd and Havenhand, 1983). These species are ecologically comparable in occupying similar niches, preying preferentially upon the same species of bryozoan [Electra pilosa (L.)], having the same (annual) life-cycle and life history (semelparous) strategies, and reproducing at much the same time of year. Both are simultaneous hermaphrodites and lay their eggs in gelatinous benthic spawn masses. They differ, however, in their egg sizes and individual fecundity (85 μm, 6-50 x 10^3, Onchidoris; 170 μm, 2-40 x 10^2, Adalaria) and larval type: Onchidoris has long-term planktotrophic larvae (Todd and Havenhand, 1985), while Adalaria has briefly pelagic lecithotrophic veligers. Adalaria larvae can feed, but do not require to do so in completing development and metamorphosis; the larvae are pelagic for perhaps a minimum of 1-2 days and will only metamorphose on contact with the live bryozoan prey (Thompson, 1958). Onchidoris, on the other hand, undergoes an extended pelagic phase metamorphosing after perhaps 35 days in the plankton (Todd and Havenhand, 1985). The contrasts in egg size and larval type thus confer markedly different egg to benthic juvenile periods, at the same temperature, and contrasting larval transport potential.

Previous analyses of these species showed two striking features. First, the lecithotrophic strategy correlated with an absolutely higher (but relatively lower) level of caloric investment, and second, there is a highly significant allometric relationship between body size and fecundity in Onchidoris murciata but only a marginally significant relationship for Adalaria proxima (Todd, 1979a; Todd and Havenhand, 1983). For the analysis of spawn calories (y) on body calories (x) the regression coefficients, r^2, n, and significance levels were: O. muricata, 1.83, 0.64, 15, $P < 0.001$; A. proxima, 0.34, 0.25, 19, $P < 0.05$. Thus, larger individuals of Adalaria generally produce fewer offspring on a weight-for-weight basis than do smaller conspecifics. Indeed, for Adalaria only 25% of the variance in individual fecundity is explained by variation in body size, by contrast to 65% for Onchidoris.

There are reasons to suggest that these two species share a recent common evolutionary ancestry (Havenhand et al., 1986) and that Adalaria is the more advanced derivative. The question to be resolved, therefore, is why Adalaria should have been selected for lecithotrophy. It was previously suggested (Todd, 1979a) that this relinquishing of planktotrophy could concern an adaptive response to the above mentioned unpredictability of energy diversion to reproduction in Adalaria adults; the lecithotrophic strategy is presumed to confer the higher probability of individual larval survival to metamorphosis. In consequence lecithotrophy might comprise the 'safer' mode of reproduction by decreasing individual variance in reproductive success.

MATERIALS AND METHODS

The primary objective of this study was to analyse the effects of differing levels of energy availability ("ration level") during the reproductive period on: (1) measurable fitness components (e.g. spawn mass sizes and numbers, total reproductive allocation); (2) survivorship; and (3) copulatory activity for isolated pairs of these molluscs. This approach is ecologically valid in view of the decidedly patchy distribution of the prey bryozoan. Three ration levels were adopted. The first grouping concerned "fully-fed" control pairs, in which nudibranchs were fed ad libitum in a manner consistent with that prior to the onset of spawning for all pairs. The second was a "half-ration" grouping, in which pairs, immediately following first spawning, were provided with Electra for a period of days, starved for a similar period, and re-fed/starved for a differing period, and so on. All pairs for both species at half-ration encountered the same sequence of availability/unavailability of Electra following their first spawning. Periods were selected from random digit tables with the objective of providing the nudibranchs with unpredictable access to Electra which, over the (then unknown) duration of the spawning period, would result overall in an ≈50% availability. The third was a "starved" grouping in which molluscs were denied Electra throughout, following first reproduction for each pair. The data concern, for Adalaria

15, 10 and 8 pairs, and for *Onchidoris* 13, 10 and 12 pairs in the "fully-fed", "half-ration" and "starved" treatments respectively.

Pairs of nudibranchs were maintained throughout in small mesh cages placed in the one aquarium, through which fresh seawater (at ambient field temperatures) flowed continuously to waste. Food was provided as *Electra* colonies epiphytic on *Fucus serratus* (L.). Cages were inspected daily with observations of copulatory activity being made and, where appropriate, spawn masses removed and food changed. When *Electra* was added the nudibranchs were placed on the bryozoan itself and, if copulating, care was taken to not separate the pair during transfer.

Spawn masses were examined for fertility and if cleavage had not commenced the diameters of ten zygotes were measured to the nearest micrometre. Every spawn mass was then mounted between glass slides and a silhouette projected using a photographic enlarger. This permitted the error-free enumeration of all eggs. Egg totals for all spawn masses were converted to dry weights, and thence caloric (joule) equivalents using previously derived predictive regressions (Todd, 1979a). Individual nudibranchs were regularly damp-weighed to provide body sizes of reproducing adults and, again, these converted to their joule equivalents (Todd, 1979a). Body sizes were invariably maximal at the commencement of reproduction. Reproductive effort was quantified as the turnover ratio [Total spawn joules ÷ maximum post-spawning body joules (for the pair) x 100] used previously (Todd, 1979a; Todd and Havenhand, 1983; see Hall and Todd, 1986 for further discussion). For logistic reasons it was impracticable to monitor a sufficient number of replicates of both species at either ration level in any one year. Accordingly, data for each ration level were collated in 1979, 1981 and 1982, with the fully-fed (control) pairs being supplemented by observations from a previous study (Todd, 1979a). Locations of the field sources for both species are given in Todd and Havenhand (1983).

Because the variation in most of the parameters considered below was non-normal both inter- and intra-specific comparisons were undertaken non-parametrically using Mann-Whitney U-tests. For convenience the data for the respective species are graphically presented as 'reproductive responses': that is, the half-ration and starved treatments expressed as a proportion of the respective control groupings. (The outcomes of the U-tests are not altered by such standardization.) Throughout the analyses median (not mean) values were utilised and these are plotted together with their respective upper and lower quartiles, as indicative of variances.

Among the criteria evaluated for each pair in the respective groupings, total spawnings and egg total are self-explanatory, but the remainder require qualification: Number of copulations — Copulation was first observed usually some days prior to first spawning, and continued throughout the spawning period. The present analyses concern only those copulations following first spawning; Copulation days — This is a truncated measure of reproductive longevity, in being the number of days from first spawning to first death; Days between copulations — This was determined by dividing copulation days by number of copulations for each pair; Spawning days — This is the sum of the two periods from first spawning to first and second deaths for each pair and is, therefore, a measure of reproductive longevity; Days between spawnings — This is similar to days between copulations; Egg total, minus first spawnings — Because the half-ration and starved treatments were initiated only following first spawning, the more appropriate evaluation of fecundity, spawn size, and reproductive effort is with the first spawn masses excluded; Daily reproductive allocation in relation to ration taken — While the analyses of the above characteristics in isolation should prove informative, this study focuses on the overall day-to-day "performance" of the reproducing adults adjusted for body size and longevity. The rationale is that although senescence and death are innately determined, extrinsic mortality agents may act at any time. "Ration taken" is a composite of the ration available (1.0, 0.5 or 0) scaled downwards in making allowance for copulatory activity during periods of *Electra* provision; feeding does not, apparently, continue during coupling (pers. obs.). Because nudibranchs were inspected only once daily it has been assumed for present purposes that copulating pairs did not feed on that day (if food was actually available at half-ration), and that pairs not copulating would have fed whenever *Electra* was provided. Clearly, the latter may not pertain but any bias (for the control and half-ration pairs) should be similar throughout. Although variable both within- and between-species, the rate of egg production towards the end of the spawning period generally decreases somewhat (Todd, 1979a, Todd and Havenhand, unpubl. obs.); for convenience these allocations were assumed to remain constant and hence are simply expressed as spawn $J \cdot body\ J^{-1} \cdot day^{-1}$.

RESULTS

No significant differences (U-tests) were found for body sizes between treatments for *Onchidoris,* but a marginally significant (p = 0.042) difference was observed between the control and starved pairs for *Adalaria*; here, the median joule equivalents for fully-fed and starved pairs were 668J and 396J respectively. Within- and between-group differences in body sizes within species should not, however, markedly affect the analyses.

The outcomes of the intra- and inter-specific comparisons for the data presented in figures 1 and 2 are summarized in Tables 1 and 2, respectively. The between-treatment tests for the two species (Table 1) apply equally to the untransformed and control-standardized data. The comparisons in Table 2 are, however, based upon the standardized values: in essence, these tests evaluate whether or not the two species differed (at half-ration or starved) in their proportional responses scaled to the median value observed for their respective control groupings. Attention should also be drawn to the frequently high variances observed for the rather small sample sizes.

NUMBER OF COPULATIONS (Fig. 1a)

Copulation of some pairs was frequently scored for up

Table 1. Outcomes of U-tests between treatments for both species for the variables considered in the text and illustrated in Figures 1 and 2 (see text for details). Where significant differences were observed the ration grouping showing the greater value is also indicated (* = P<0.05; ** = P<0.01; *** = P<0.001; ns = not significant).

	Fully-fed vs. Half-ration (1.0 vs. 0.5)		Half-ration vs. Starved (0.5 vs. 0)		Fully-fed vs. Starved (1.0 vs. 0)	
	Adalaria proxima	*Onchidoris muricata*	*Adalaria promixa*	*Onchidoris muricata*	*Adalaria proxima*	*Onchidoris muricata*
Number of copulations	**FF<HR	ns	ns	**HR>S	ns	ns
"Copulation days"	ns	ns	ns	ns	ns	ns
Days between copulation	*FF<HR	ns	ns	**HR<S	ns	**FF>S
Total spawnings	ns	ns	ns	**HR>S	*FF>S	***FF>S
"Spawning days"	ns	ns	ns	ns	ns	**FF>S
Days between spawnings	ns	ns	ns	**HR<S	ns	*FF<S
Egg total	ns	ns	**HR>S	**HR>S	**FF>S	***FF>S
Egg total, minus first spawnings	ns	ns	*HR>S	**HR>S	**FF>S	***FF>S
Spawn size, minus first spawnings	ns	*FF>HR	*HR>S	**HR>S	**FF>S	***FF>S
Reproductive effort, minus first spawnings	ns	ns	*HR>S	*HR>S	**FF>S	***FF>S

Table 2. Inter-specific outcomes of U-tests for both the "half-ration" and "starved" treatments (standarised on their respective species' "control" groupings) in terms of the variables compared intra-specifically in Table 1. (*A.p.* = *Adalaria proxima*; *O.m.* = *Onchidoris muricata*; * = P<0.05; ** = P<0.01; ns = not significant).

	Half-ration	Starved
Number of copulations	*A.p. > O.m.*	ns
"Copulation days"	*A.p. > O.m.*	ns
Days between copulations	ns	ns
Total spawnings	ns	ns
"Spawning days"	**A.p. > O.m.*	ns
Days between spawnings	ns	ns
Egg total	ns	**A.p. > O.m.*
Egg total, minus first spawnings	ns	ns
Spawn size, minus first spawnings	ns	ns
Reproductive Effort, minus first spawnings	ns	ns

to six consecutive days. For analytical purposes each daily observation was considered a separate event although it would not be possible to distinguish these from a single protracted coupling.

DAYS BETWEEN COPULATIONS (Fig. 1c)

For both species there were overall trends of decreases in the intervals between copulations. Whether this is attributable to an increase in frequency or duration of copulation cannot be ascertained but the net effect is that at reduced ration the nudibranchs engage in this non-energy-acquiring activity to a greater extent. In view of the importance of continued feeding to reproductive allocation this is, therefore, a possible cost to fitness.

EGG TOTAL, MINUS FIRST SPAWNINGS (Fig. 2h)

The outcome for this criterion remains almost unchanged (with respect to g.) although the significant inter-specific difference (Table 2) is lost.

SPAWN SIZE, MINUS FIRST SPAWNINGS (Fig. 2i)

Figure 3 illustrates the frequency distributions of spawn mass sizes within each treatment for both species and distinguishes the first spawn masses from those subsequently laid. Strikingly similar patterns of response to ration level were noted for both species. The summed first two spawn masses produced by each pair did not differ significantly between treatments for either species (P ranging from 0.135 to 0.644), but the size and absolute number of subsequent spawnings declined very significantly (P<0.001). Egg sizes did not differ significantly between the treatments for *Onchidoris* but *Adalaria* showed a more variable pattern (Table 3). Nevertheless, the possibility remains that energy density per egg declines with ration: this could have incurred slight overestimates of spawn caloric equivalents at reduced ration.
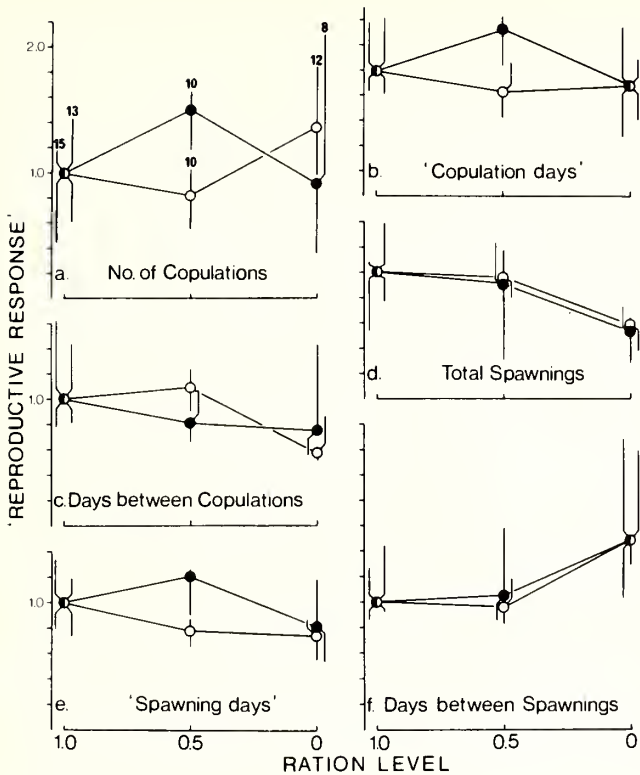
Fig. 1. Responses of *Adalaria proxima* (infilled circles) and *Onchidoris muricata* (open circles) to the half-ration (0.5) and starved (0) treatments, expressed as a proportion of their fully-fed (1.0) controls. Values are medians, with upper and lower quartiles also indicated. The number of replicate pairs for each species are given in figure 1a.
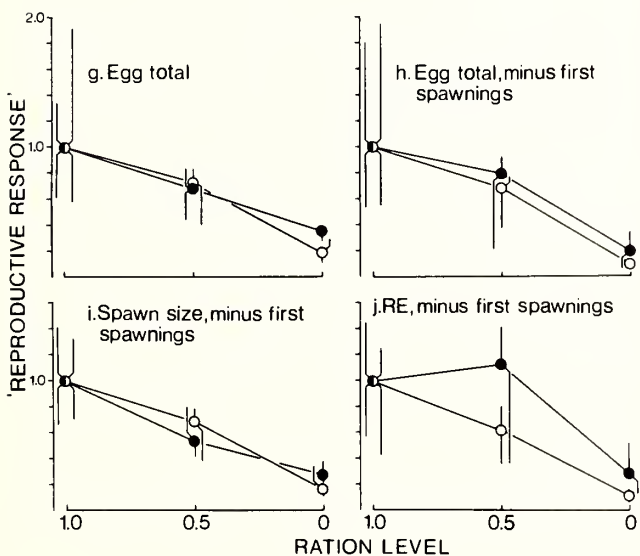

Fig. 2. Further reproductive responses of *Adalaria proxima* and *Onchidoris muricata* to the dietary treatments, as in figure 1. (RE = Reproductive Effort).
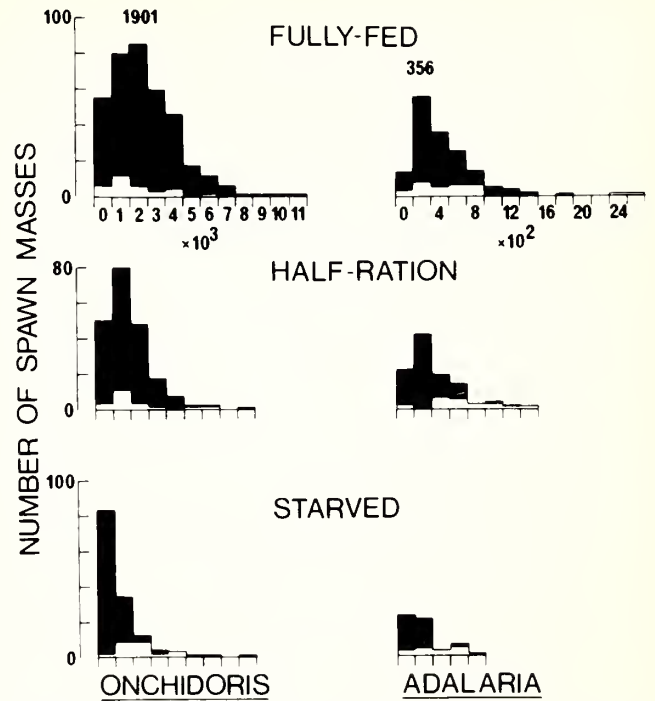

Fig. 3. Histograms of spawn mass sizes for all groupings of both species. Values on the abscissa show the number of eggs per spawn mass and in all cases are mid-points of the size-classes. The unshaded components in the histograms indicate the summed first two spawn masses for pairs in each grouping. Median sizes of spawn masses in the control groupings are also given for each species.

REPRODUCTIVE EFFORT (RE), MINUS FIRST SPAWNINGS (Fig. 2j)

The variances in these data are particularly large. However, in view of the poor relationships between body sizes and fecundity (see Introduction), the especially high variance for *A. proxima* at half-ration is unsurprising. These data provide further evidence of the inadequacy of simple turnover ratios in expressing individual reproductive "effort".

DAILY REPRODUCTIVE ALLOCATION, IN RELATION TO RATION TAKEN (Fig. 4)

As outlined above, the most appropriate analysis concerns the data with the first spawnings deleted. For comparative purposes figure 4 includes plots both "inclusive" and "exclusive" of these spawnings. For *Adalaria* no significant differences between treatments were noted for the inclusive data; for the exclusive plot there were no significant differences between adjacent groupings, but there was a significant ($P < 0.05$) decrease in daily allocation for starved versus control pairs. For *Onchidoris* there was no significant difference between the fully-fed control and half-ration pairs, but a marked and significant ($P < 0.001$) decrease in allocation for the starved treatment. On a weight-for-weight basis, the two species' daily allocation to reproduction were

remarkably similar on starvation, despite *Adalaria* being perhaps up to five times larger. Although *A. proxima* does produce fewer (up to 8) spawn masses than *O. murciata* (up to 19), the greater reliance of *Adalaria* on the earlier spawn masses, in maximizing overall fecundity, is clearly seen from the inclusive and exclusive plots. Resources for these spawnings are accreted over some weeks or months prior to the initiation of spawning. By contrast, the dependence of *Onchidoris* upon recurrent energy intake during the reproductive period is also evident in this figure: clearly, RE values approaching and exceeding 100% (Todd, 1979a; Todd and Havenhand, 1983) can only be supported by such continued feeding. *Adalaria* is, however, considerably less compromised by ration level but, as figures 1 and 2 clearly demonstrate, both reduced and zero energy availability do exert quantifiable contraints on behaviour and fitness. Owing to the patchy and discontinuous distribution of bryozoan prey colonies it is likely that the half-ration regime is not that dissimilar to field circumstances, and such would appear borne-out by figure 4.

Smaller spawn masses for both species comprise fewer embryos/total caloric content than do larger masses (Fig. 5): this is accounted by each egg requiring a minimum (gel) protection and there being a basic caloric cost in constructing a spawn mass. The 'cost per egg' curves decline asymptotically to a size beyond which it becomes no 'cheaper' to package the eggs. Also indicated are the median spawn mass sizes recorded for the summed fully-fed groupings: in each case the nudibranchs are, at least as groups, generally producing the smallest masses which provide the greatest number of larvae per joule invested.

Consideration of the range of characteristics independently (Figs. 1, 2) shows that, in general, both species responded similarly (on a proportional basis, scaled to the fully-fed controls) to a reduced or zero availability of energy (food) during the reproductive period. Despite the considerable variances distinct patterns of response are apparent. Survivorship, spawn numbers, and spawn sizes all showed, to a greater or lesser extent, decreases with ration level, and intervals between spawnings were particularly increased at zero ration. Perhaps an unexpected outcome was the increase in the proportion of time that the half/zero ration pairs engaged in copulation. Feeding does not, apparently, continue during coupling (pers. obs.). Certainly, for organisms dependent (albeit to differing degrees) upon recurrent energy intake in maximising fitness, such a response
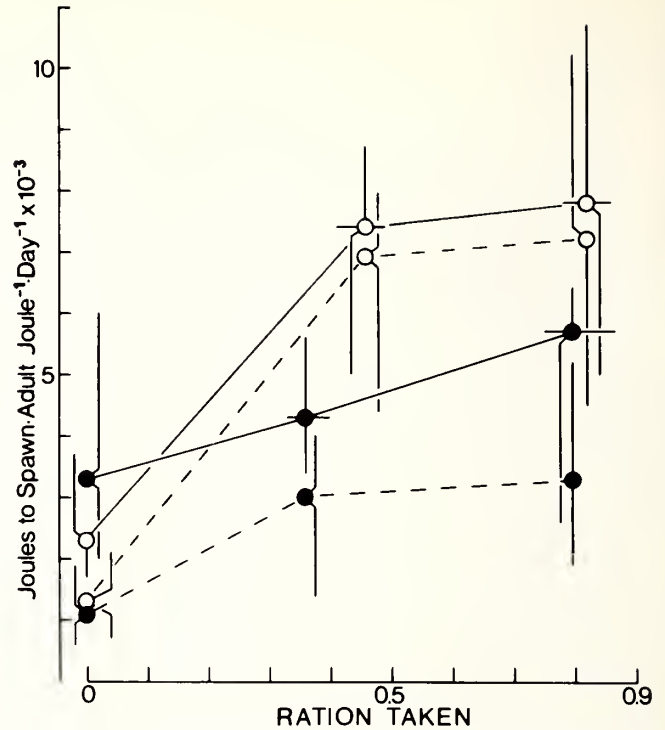

Fig. 4. Daily reproductive "performance" of the two species at varying ration level, scaled for body size and duration of spawning periods. Median values with upper and lower quartiles are shown. Broken plots refer to data from which the first two spawn masses produced by each pair have been excluded.

was unexpected. Several possible explanations could be advanced, the second of which is presently being experimentally evaluated: 1. Copulation can normally be concluded when the bursa copulatrix is filled, and this can take longer under energetic stress. Certainly, individual oxygen consumption rates decrease markedly upon starvation (unpubl. pers. obs.); 2. Individuals under such stress can catabolize allosperms in the gametolytic gland, and use the products metabolically. The suggestion here is one of individuals attempting to maximize intake by increasing copulatory activity; 3. Energetic stress presumably affects the female function more than the male: the increase in copulation can,

Table 3. Mean egg diameters ± 2 standard errors for both species at the three ration levels. n denotes the number of spawn-masses concerned and bars (for *A. proxima* only) indicate significant differences (P < 0.05, U-test) between groupings.

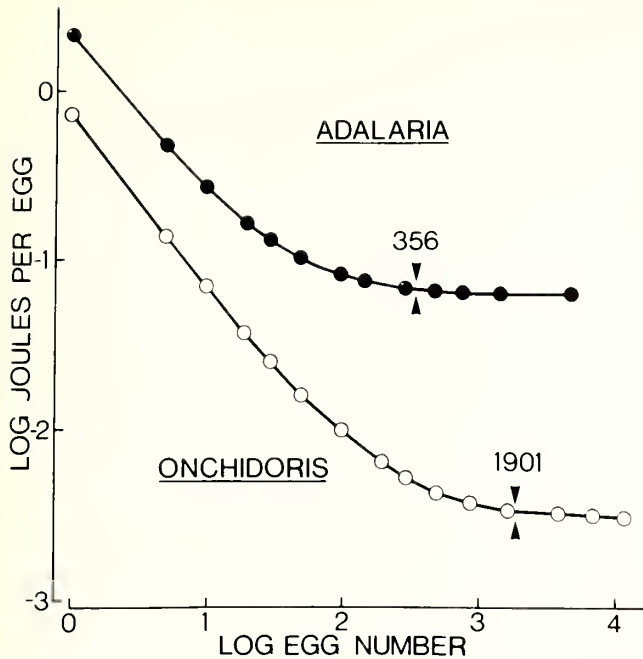|	Fully-fed	Half-ration	Starved
Onchidoris muricata	83.0 $\pm$ 1.9 μm, n = 18	84.2 $\pm$ 1.9 μm, n = 13	84.6 $\pm$ 1.5 μm, n = 16
		(No significant differences between groupings)	
Adalaria proxima	167.1 $\pm$ 1.4 μm, n = 38	171.6 $\pm$ 2.7 μm, n = 10	163.1 $\pm$ 1.7 μm, n = 49

Fig. 5. Relationship between the "cost per egg" in various spawn masses of the range of sizes predicted for each species on the basis of caloric conversions (see Todd, 1979a). The median spawn mass size (control groupings only) for each species is also indicated. See text for further details.

therefore, simply be a response of the individual maximizing its own fitness through its male function.

DISCUSSION

For those organisms which produce more than one clutch or spawn mass during the reproductive period, food availability to the adult is likely to be of crucial importance to not only later offspring production, but also parental survivorship. Most investigations of the effects of ration on reproduction have concerned fish (e.g. Bagenal, 1969; Wootton, 1973, 1977; Reznick, 1983), but data are available for lizards (e.g. Ballinger, 1977), insects (e.g. Collins, 1980; Moeur and Istock, 1980), nematodes (Schiemer et al., 1980) triclads (e.g. Calow and Woollhead, 1977; Woollhead, 1983), and other molluscs (O'Dor and Wells, 1978; Scheerboom, 1978; Russell-Hunter et al., 1984). To date, the only comparable data for a nudibranch concerns Smith and Sebens' (1983) investigation of Onchidoris aspera (L.) in New England.

In the case of invertebrates which continue to grow while still reproducing it is apparent that there will be different thresholds of ration necessary to maintain both growth and reproduction (e.g. Scheerboom, 1978). For the present nudibranchs, however, both somatic and total production rates decline during the spawning period [in contrast to, e.g. Aeolidia papillosa (L.) (Hall and Todd, 1986)] and, indeed, somatic "degrowth" is invariably observed as soon as spawning commences (unpubl. pers. obs.). Degrowth concerns the decrease in mass of any structural proteins (Russell-Hunter

et al., 1984) and is not to be confused with, for example, the inhibition of protein synthesis as a result of reproduction.

The responses of particular organisms to reduced or zero ration varies from one species to another, depending primarily upon the semelparous/iteroparous dichotomy (see, for example, Calow and Woollhead, 1977; Woollhead, 1983). However, Spight and Emlen (1976) noted increases in spawning activity for two (iteroparous) Thais species, in response to increase in food supply, while McKillup and Butler (1979) found increases in egg production with decreases in food availability in the similarly iteroparous Nassarius pauperatus McKillup and Butler. The British dorid Onchidoris muricata is probably closely related to O. aspera (studied by Smith and Sebens, 1983) and yet although O. muricata displayed reduced reproductive activity under starvation, O. aspera, under similar circumstances, failed to spawn at all. Fecundity and body size generally display some form of allometry amongst nudibranch molluscs (Todd, 1979a, b; Todd and Havenhand, 1983; Hall and Todd, 1986). Adalaria proxima is small, but up to five times larger than O. muricata. Despite the high individual variance in RE for A. proxima (see Todd and Havenhand, 1983: Fig. 1), a spawning adult could, on average, produce approximately twice as many equivalent planktotrophic larvae as does O. muricata. The question remains: why does it not do so? For A. proxima individuals the apportionment of resources toward reproduction is both highly variable and unpredictable. (For O. muricata an individual of given size will produce a more-or-less predictable number of offspring.) The suggestion is that the "safer" lecithotrophic strategy reduces the variance and maximises the probability of at least some larval success, but at what selective cost?

The definitive 'per day' evaluation of allocation in relation to ration taken (Fig. 4) demonstrates the overriding interspecific differences. The strategy of Onchidoris muricata is to maintain a small body size, degrow slowly (unpubl. obs.) and divert both recurrent energy intake and catabolic products to reproduction. Adalaria proxima, by contrast, attains a larger body size, degrows rapidly and seems comparatively incapable (in many individual cases) of exploiting recurrent energy (see Fig. 4). For adult A. proxima the situation remains one of unpredictability of allocation between components of individuals' energy budgets (especially respiration, Todd and Havenhand, unpubl. obs.). Selection for lecithotrophy as an adaptive response to this is perhaps only one solution, and one which is probably only open to A. proxima because of its absolutely greater reproductive capacity (Todd, 1979a). But this is not to say that reproduction of A. proxima is inefficient, ineffective or suboptimal, as figure 5 clearly demonstrates.

I view figure 5 as a clear example of optimised reproductive allocation, for the requisite eggs must be accumulated over a period of days and individuals produce, on average, the most efficient masses with the minimum of delay. Take two extremes: individual A produces very many small spawn masses as soon as the eggs are synthesised, while B accumulates oocytes and produces only a few very large masses. Depending upon the mortality regime to which individual spawn masses are subject it could be that hatching

success is maximised for individuals which adopt the strategy of individual B. In reality, however, both individuals would probably perform suboptimally; B may not itself survive to reproduce at all, while A constantly produces "inefficient" spawn mass sizes although maximising its daily productivity.

Much of the available data relating to larval types and reproductive allocation among Nudibranchia have been recently reviewed elsewhere (Todd, 1981, 1983; Hadfield and Switzer-Dunlap, 1984). Of late, interest has focused upon the incidence of extra-zygotic yolk reserves (e.g. Boucher, 1983, 1986; Thompson and Salghetti-Frioli, 1984), in addition to further analyses of metamorphosis of the tropical aeolid *Phestilla sibogae* Bergh (Hadfield, 1977, 1978, 1984; Hadfield and Scheuer, 1985; Kempf and Hadfield, 1985; Miller and Hadfield, 1986; Yool et al., 1986). Reproductive patterns incorporating extra-zygotic yolk appear particularly prevalent among tropical/sub-tropical Ascoglossa (see Clark and Goetzfried, 1978; Clark and Jensen, 1981; Clark et al., 1979), but also feature amongst dorid nudibranchs (Boucher, 1983). Perhaps its most striking consequence is the reduction in cleavage time and embryonic developmental rates conferred by reducing egg size (see Todd and Doyle, 1981).

The utilization of such extra-capsular nutritive reserves I view as being specializations within the usual categories of larval strategies. Notwithstanding this qualification, it is apparent that my convictions of the fundamental importance of the individuals' energetics in playing a part, or perhaps even a major role, in outlining the functional limitations and defining selection for particular larval types, are not shared by Clark and his co-workers (see e.g. Clark and Goetzfried, 1978; Clark et al., 1979; DeFreese and Clark, 1983). Rather, they have invoked the importance of climatic stability and availability/seasonality of (prey) production.

Whatever one's viewpoint, we ultimately require exhaustive investigation of survivorship of both adults and their offspring in the field, rather than just the laboratory. For example, field observations of small, isolated populations of *Onchidoris bilamellata* (L.) showed RE values of only 48 and 63%, in contrast to laboratory values ranging from 114 to 150% (Todd, 1979b). But perhaps more pressing is the need to evaluate specifically the genetic consequences (in terms of larval transport/dispersal potential) of the planktotrophic and lecithotropic strategies. They are clearly not similar means to the same end. Functional energetics could or could not explain why a particular strategy is selectively favoured in certain cases (including the present), but only within a genetic framework will the adaptive significance of these alternatives avail itself of informed judgement. Furthermore, we should be wary of the pitfall of believing in the perfectibility of genotypes. I can only echo the sentiments of Grahame and Branch (1985) in concluding their review of marine invertebrate larval strategies: "...while devising ingenious adaptive explanations for observed features, we must bear in mind that natural selection works with what is available to do only the best necessary job."

ACKNOWLEDGMENTS

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